Echinoids as hard substrates: varied examples from the Oligocene of Antigua, Lesser Antilles

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ABSTRACT

A collection of unremarkably preserved fossil irregular echinoids from the Upper Oligocene (Chattian) Antigua Formation of Antigua, Lesser Antilles, nonetheless provides evidence of a range of palaeoecological interactions. A dead test of the heart urchin *Eupatagus* sp. formed a hard substrate for the attachment of gregarious *Thecidellina*? sp., a thecidoid brachiopod. Although obligate encrusters, these brachiopods more commonly occur as disarticulated valves free of the substrate in the Antillean fossil record. Elongate pits in test fragments were formed, variously, before and after the death of the host echinoids. These depressions on the external surface were formed either by invertebrates excavating domiciles or by claws or teeth; the echinoid later reclaimed the pits and grew new tubercles in the base. Post-mortem pits lack such new tuberculation. A test of *Eupatagus* sp. bears the boring *Oichnus* isp., formed either by a predator (gastropod?) or after the death of the echinoid (domicile), and a serpulid worm tube which grew on the test subsequent to the echinoid's death. The echinoid fauna of the Antigua Formation has been easy to collect and specimens are to be found in many museums; they now await re-examination to reveal palaeosynecological data analogous to that determined from the fragments discussed herein.

1. Introduction

Poddubiuk and Rose (1985, p. 118) described the Upper Oligocene Antigua Formation of Antigua, Lesser Antilles, as "… a transgressive shallow marine limestone sequence resting disconformably on reworked pyroclastic deposits [= Central Plains Group] sometimes containing freshwater fossils." Frost and Weiss (1979, p. 612) had previously called it "… the reference unit for the marine Oligocene of the Western Hemisphere." The Antigua Formation is thus recognized as a unit of some international interest and importance, esteemed for the insights provided by its litho- and

biostratigraphy (see, for example, Weiss, 1994; Johnson, 2007).

A significant aspect of the fossil fauna of the Antigua Formation is its echinoids, a rare occurrence in a region where Oligocene echinoids remain poorly described and defined. As noted by Kier (1984, p. 6), although coeval echinoids from Cuba should be of primary importance, the confusion of Miocene and Oligocene deposits by previous authors needs to be disentangled; over 30 years later, this has yet to happen. Indeed, in the past 50 years, there are only two major studies of the Chattian (Late Oligocene) echinoids of Antillean islands, specifically, of Jamaica (Dixon, 1995) and Antigua (Poddubiuk, 1987). Only one of these has been published in full (Dixon and Donovan, 1998), although Poddubiuk and Rose (1985, table 1) did provide a faunal list. An illustrated field guide to the fossil echinoids of Antigua is now in the early stages of preparation (S.K.D. and R.W.P., research in progress).

However, prior to such a major systematic treatment, we present a short examination of aspects of the palaeoecology of the echinoids of the Antigua Formation, most particularly their use by other marine invertebrates as hard substrates, both pre- and post-mortem. The utilization of echinoderms as hard substrates by other invertebrates is widely recognized from the fossil record (see, for example, Donovan, 1991, 2015; Nebelsick et al., 1997; Zamora et al., 2008; Jagt et al., 2012; Borszcz et al., 2013; Mancosu and Nebelsick, 2015), although such studies have yet to be common from the Cenozoic of the Antilles. Herein, we examine the evidence provided by three distinct examples of echinoid-invertebrate interactions as part of a wider study of the fossil record of the island of Antigua.

Terminology of the echinoid endoskeleton follows Melville and Durham (1966) and Smith and Kroh (2011). Our philosophy of open nomenclature follows Bengtson (1988). The specimens discussed herein are deposited in the Florida Museum of Natural History, University of Florida, Gainesville (UF).

2. Localities and horizons

This section is adapted in part from Donovan et al. (2015, pp. 291—292). Antigua is about 280 km^2 in area and forms part of the northern Lesser Antilles volcanic arc. The northern Lesser Antilles are formed of a double volcanic arc which diverges northwards (Wadge, 1994). To the west are the northern (and younger) Volcanic Caribbees, a line of islands formed by volcanoes during the Neogene, some of which are still active. To the east are the Limestone Caribbees, islands that were volcanic in origin, but which are older (mid-Cenozoic) and are now dormant. Antigua is a Limestone Caribbee.

Antigua's rock succession is a record of the transition from island arc volcanism to quiescence and limestone deposition. This change happened during a relatively short geological interval, the Late Oligocene (Chattian); that is, the island's rock succession was deposited during part of a 6-million-years slice of the Paleogene. Lithofacies belts reflect deepening to the north-west (Fig. 1). The geological environment evolved from a number of active volcanoes that were erupting sub-aerially in the south and west (Basal Volcanic Suite; Tomblin, 2005); through terrestrial and near-shore marine sandy environments, the sediment being derived by erosion and redeposition of the volcanic rocks, with minor limestones (Central Plains Group); to offshore limestone environments that included deeper water settings of over 150 m water depth (Antigua Formation) (Martin-Kaye, 1959; Weiss, 1994; Jackson & Donovan, 2013; Donovan et al., 2014). It is the limestones of the Antigua Formation that form the subject of the present study.

2.1 Locality 1

The north-east point of Half Moon Bay, parish of Saint Philip, south-east Antigua (Fig. 1, 2A), exposes 8+ m of the Antigua Formation as a series of benches. These well-lithified limestones have yielded a suite of fossils indicative of deeper water deposition in, probably, 150+ m. The fauna, including allochthonous elements, consists of calcareous algae, articulated sponges, brachiopods, crinoid columnals, echinoids, asteroid marginal ossicles, rare oysters, scallops and other benthic molluscs, and trace fossils (Donovan et al., 2015, 2017; Strang et al., in press). Foraminiferans from these beds include flat *Lepidocyclina canellei* Lemoine and Douvillé and inflated *Eulepidina* sp. cf. *E.*

undosa (Cushman). All specimens discussed herein come from this locality (Figs 3, 4B-D, F) except UF 277887 (Fig. 4A, E).

2.2 Locality 2

The limestones exposed on the coast to the east of Boon Point, parish of Saint John, north coast of Antigua (Fig. 1), are less extensive both laterally and stratigraphically than those of Locality 1. These beds are particularly well-lithified and relatively sparsely fossiliferous, although it has been a fruitful site for decapod crustaceans (R.W.P., research in progress), benthic molluscs (epitoniids), foraminifers and echinoderms (cidaroids, spatangoids, asteroid marginal ossicles). In the absence of other palaeontological indicators, these limestones are presumed to have been deposited in shallower water than Locality 1, although still deep enough to have engendered meandering burrows (Fig. 2B), perhaps the spoor of *Eupatagus* sp. (Fig. 4A) and close to *Olivellites* isp. The meandering trace may be indicative of a deep water setting.

3. Descriptions

3.1 UF 277885 (Figs 3, 4C, F)

This specimen is an incomplete spatangoid echinoid (heart urchin), probably *Eupatagus* sp. of Poddubiuk and Rose (1985, table 1). This thin-tested specimen has been flattened, presumably by the weight of overburden, and has cracked around the ambitus. Part of the apical surface is exposed, including an area of large, crenulate, perforate tubercles adapical of the peripetalous fasciole. The two ambulacral petals partially exposed are identified as the right and left anterior ambulacra (= ambulacra II and IV, respectively). In Figure 4C, the apex of the test is situated near the top centre and the anterior, non-petaloid ambulacrum (III) is angled from here to right of the bottom left-hand corner; however, it is less distinctive than the petals.

Cemented to this surface are two valves each derived from an attached brachiopods, a

thecidoid sp. indet., one more prominent than the other (Fig. 3). The prominent valve is on the left anterior interambuacrum (= 3) in the area dominated by large primary tubercles (Figs 3, 4C, F). The second attached valve overlaps ambulacrum III and the right anterior interambulacrum (= 2) (Figs 3, 4C, right of centre in both images). A faint rounded structure (not apparent in the figures) in ambulacrum III may be a juvenile.

3.2 UF 277886, 279143 (Fig. 4B, D)

Both specimens are small fragments of the tests of spatangoid echinoids. There are three lozenge-shaped pits in UF 277886 (Fig. 4D; third pit not illustrated) on two large interambulacrum plates. These pits are shallow, irregularly oval to elongate hexagonal in outline and 5 mm or less in length. The bases of these pits have a similar tuberculation to the adjacent echinoid test (Fig. 4D).

The pit on UF 279143 has a more angular, irregularly pentagonal outline. It lacks tubercles on its smooth floor and the edges of the pit are more angular than those of UF 277886 (compare Fig. 4B, D).

3.3 UF277887 (Fig. 4A, E)

Eupatagus sp. is the most complete echinoid considered herein (Fig. 4A), but is still poorly preserved. The apical surface of this test preserves two structures of note. The posterior column of pore pairs of the posterior right ambulacral petal (= ambulacrum I) is perforated by a small round hole referred to *Oichnus* isp. (Donovan and Pickerill, 2017). Close to the apex of the left posterior ambulacrum (= V) and left lateral interambulacrum (= 4) is a poorly preserved serpulid worm tube.

4. Discussion

The specimens described above provide varied evidence of interactions between live and dead

echinoid tests, and other invertebrates, and will be considered in the same order as above. The *Eupatagus* sp. test encrusted by thecidoids sp. indet. must have been dead at the time of infestation, as the brachiopods overgrow tubercles that would have borne spines in life. These had to be lost before this this surface could be infested by encrusting brachiopods (=episkeletozoans *sensu* Taylor and Wilson, 2002). This gregarious association of thecidoids is unexpected for two reasons. Neither thecidoids nor other encrusting brachiopods have hitherto been identified from the Oligocene of the Antillean region (Cooper, 1979, p. 28; Harper, 2002, figs 12.2, 12.3) apart from *Lacazella* sp. indet. recorded with uncertainty from Puerto Rico (Harper, 2002, table 12.1). Further, thecidoids from the Antilles may be found as disarticulated valves or articulated shells, but they are commonly not found attached to a substrate (for example, in the Mio-Pliocene of Curaçao; Harper et al., 2003).

The small, ventral shells of the thecidoid are partially dissolved, removing details of the ventral interarea, teeth and apex of the valves. The shells are tentatively assigned to *Thecidellina*? sp. pending more data on the ventral valve and information on its dorsal interior. *Thecidellina* Thomson commonly occurs together with *Lacazella* Munier-Chalmas in the tropics (see Grant, 1987) forming an ecological association of low-level, cemented suspension feeders. Fossil species of *Thecidellina* and *Lacazella* occurred, at low-latitudes, in the Paleocene and Eocene of Alabama (Cooper, 1979, 1988), the Eocene and Oligocene of the circum-alpine region (Nebelsick et al., 2011), the Eocene and Miocene of Cuba, the Miocene of Australia (Lee and Robinson, 2003) and Java (Cooper, 1978), and the Pleistocene of Vanuatu (Cooper, 1978). *Thecidellina* is cosmopolitan within the warmer waters of the tropics and substropics, commonly restricted to cryptic environments at depths from some few metres to 150 m, today and presumably in the past. Species are generally cemented by their ventral valves to rock and corals, more occasionally to other brachiopods and serpulid worm tubes (Jackson et al., 1971; Lee and Robinson, 2003). The occurrence of the *Lacazella-Thecidellina* association in the Oligocene is rare and the attachment of the brachiopod to an echinoid test, unusual. However, the presence of *Thecidellina*? sp. in a deeper water

palaeoenvironment is in keeping with other Cenozoic brachiopods in the Antillean region (Harper, 2002; Donovan et al., 2015).

Rather different associations are presented by the two pitted test fragments (Fig. 4B, D). The pits are of uncertain origin, either domiciles of pit-forming organisms (compare with Donovan and Tenny, 2015), tooth marks (compare with Donovan et al., 2010) or mechanical damage. The pits in UF 277886 (Fig. 4D) must have been made when the echinoid was alive as subsequently it partly repaired the damage by growing new tubercles. These are most likely evidence of unsuccessful predation, perhaps by the teeth of a fish or the claws of a decapod crustacean (compare with Kowalewski and Nebelsick, 2003). In contrast, the broadly similar pit in UF 279143 (Fig. 4B) shows no such evidence of repair. It was therefore formed post-mortem, either between death of the echinoid and final burial, or it may be modern mechanical damage, made after exhumation of the specimen, but before it was collected.

The damage to *Eupatagus* sp. test, UF 277887 (Fig. 4A, E), has destroyed any fine morphological features of *Oichnus* isp. that would have enabled confident assignment to a nominal ichnospecies. This either represents a predatory borehole made, most probably, by a gastropod (Bromley, 2004, pp. 466-467) or was made after the death of the echinoid by an invertebrate using the test as a domicile. Presumably it was easier to bore through the pore pairs than through the solid test (Donovan et al., 2016).

The serpulid worm tube on the test undoubtedly represents encrustation of the dead test (episkeletozoan). The dense adapical tuberculation of the test (Fig. 4A) indicates that it supported a thick 'forest' of protective spines in life, which would have prevented encrustation. These would have been supported by aggressive pedicellariae which would have actively removed settling larvae (Smith, 1984, pp. 98-100).

These specimens show that even poorly preserved fossil echinoids can provide significant palaeoecological data. Because of the importance of the microfossils and invertebrates of the Antigua Formation for international correlation, and the relative ease with which the abundant macrofauna can be collected, many major museums have extensive collections from this unit. Yet the macrofauna

remains understudied; just because fossils are easy to collect in the field does not necessarily translate into published descriptions unless there is an interested expert involved with their curation. Further, such collections of museum quality will be focussed on complete, clean specimens which are not likely to be the optimum for the sort of palaeoecological study described herein (see also Thomka et al., 2016). Indeed, only the coral faunas of the Antigua Formation have received such detailed study (for example, Frost and Weiss, 1979; Johnson, 2007). We therefore advocate a 'new look' at the macrofauna of the macrofauna of the Antigua Formation preserved in museums, looking carefully at the relationships between organisms as well as their systematics.

In conclusion, the fossil echinoids of the Upper Oligocene Antigua Formation preserve diverse evidence of both live and dead tests forming hard substrates for a range of biotic interactions (Table 1). Although this must be considered a preliminary assessment, the abundant macrofauna of this formation promises to supply a wealth of palaeosynecological information that has been largely ignored hitherto.

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Table 1

A summary of palaeoecological data determined for echinoid/organism interactions from the Antigua Formation. All echinoids were spatangoids (heart urchins).

	Association	**Echinoid dead/alive?**	**Illustration**
UF 277885	encrusting brachiopods	dead	(Figs 3, 4C, F)
UF 277886	pits/invertebrate?	alive	(Fig. 4D)
UF 277887	*Oichnus*/predatory snail	alive?	(Fig. 4A, E)
	encrusting serpulid	dead	(Fig. 4A)
UF 279143	pit/mechanical damage?	dead	(Fig. 4B)

FIGURE CAPTIONS

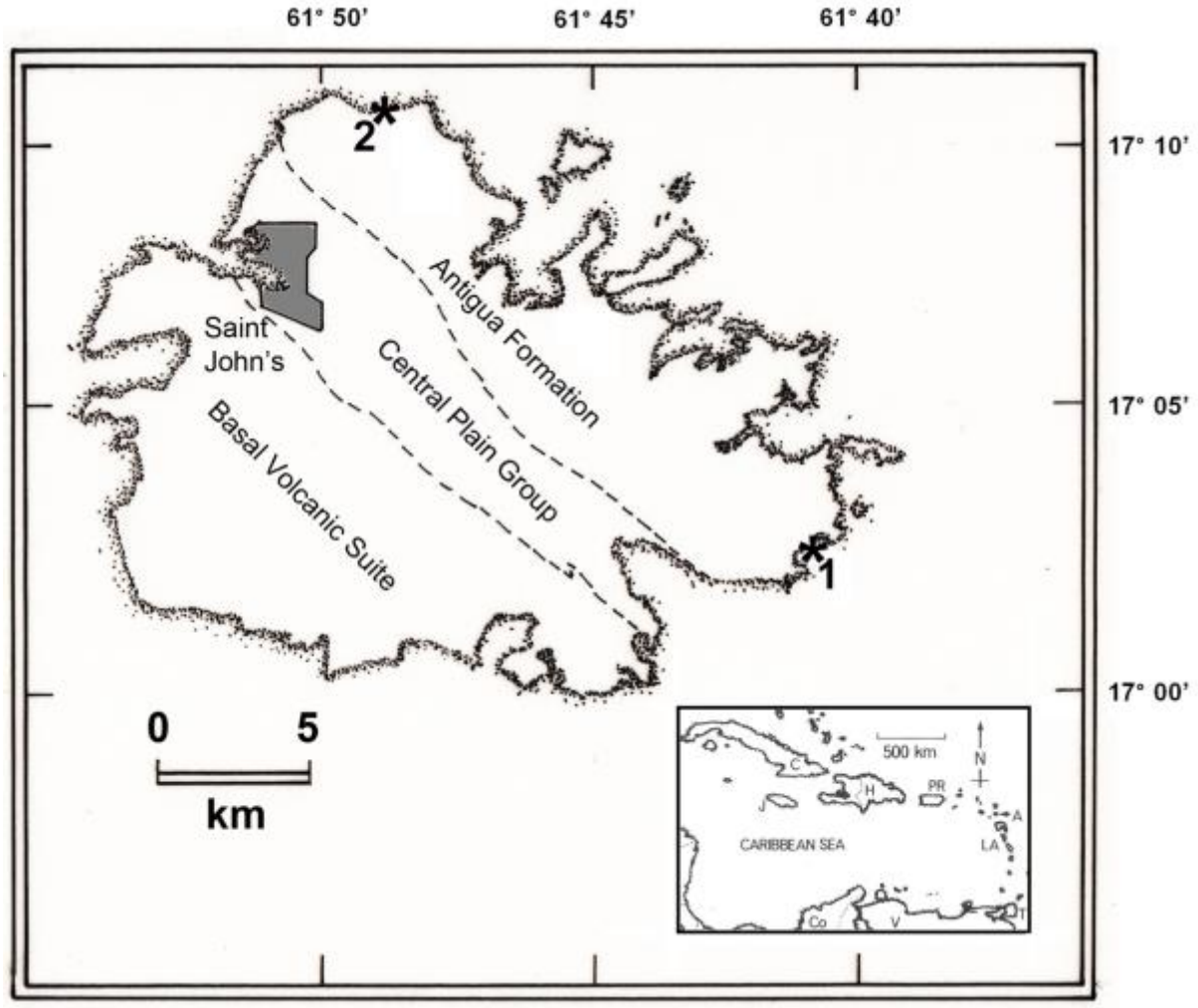

Fig. 1. Outline map of Antigua (redrawn and modified after Weiss, 1994, fig. 3), showing the principal geological subdivisions and the city of Saint John's. Key to localities: 1 = north-east point of Half Moon Bay, parish of Saint Philip, south-east Antigua; 2 = Boon Point, parish of Saint John, north Antigua. All localities in the Antigua Formation (Upper Oligocene).

Inset map shows the position of Antigua in the Caribbean. Key (clockwise from Jamaica): J=Jamaica; C=Cuba; H=Hispaniola (Haiti+Dominican Republic); PR=Puerto Rico; A = Antigua (arrowed); LA=Lesser Antilles; T=Trinidad; V=Venezuela; Co=Colombia.


A

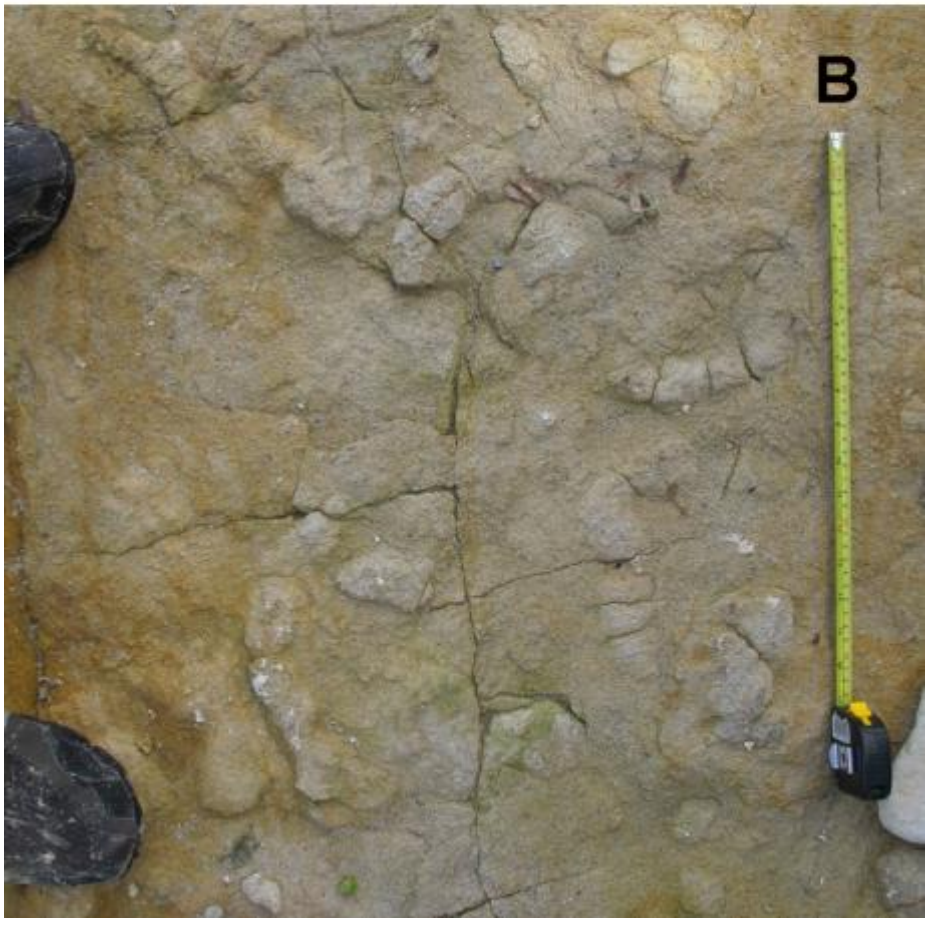
B

Fig. 2. (A) Locality 1, north-east point of Half Moon Bay, parish of Saint Philip, south-east Antigua [NGR 337 838] (after Donovan et al., 2015, fig. 2A). All beds are rich in fossil echinoderms (echinoids, isocrinid columnals, asteroid marginal ossicles). R.W.P. (white shirt, left) and D.A.T.H. (yellow shirt, centre) for scale. (B) Locality 2, robust, meandering, bedding-parallel burrows in limestones near Boon Point, parish of Saint John, north Antigua. These are reminiscent of *Olivellites* Fenton and Fenton, 1937 (see also Yochelson and Schindel, 1978; Eagar et al., 1985), included within the '*Scolicia* group' of Häntzschel (1975, p. W106), but not synonymized (see also Smith and Crimes, 1983); these are probably indicative of a deeper water environment.

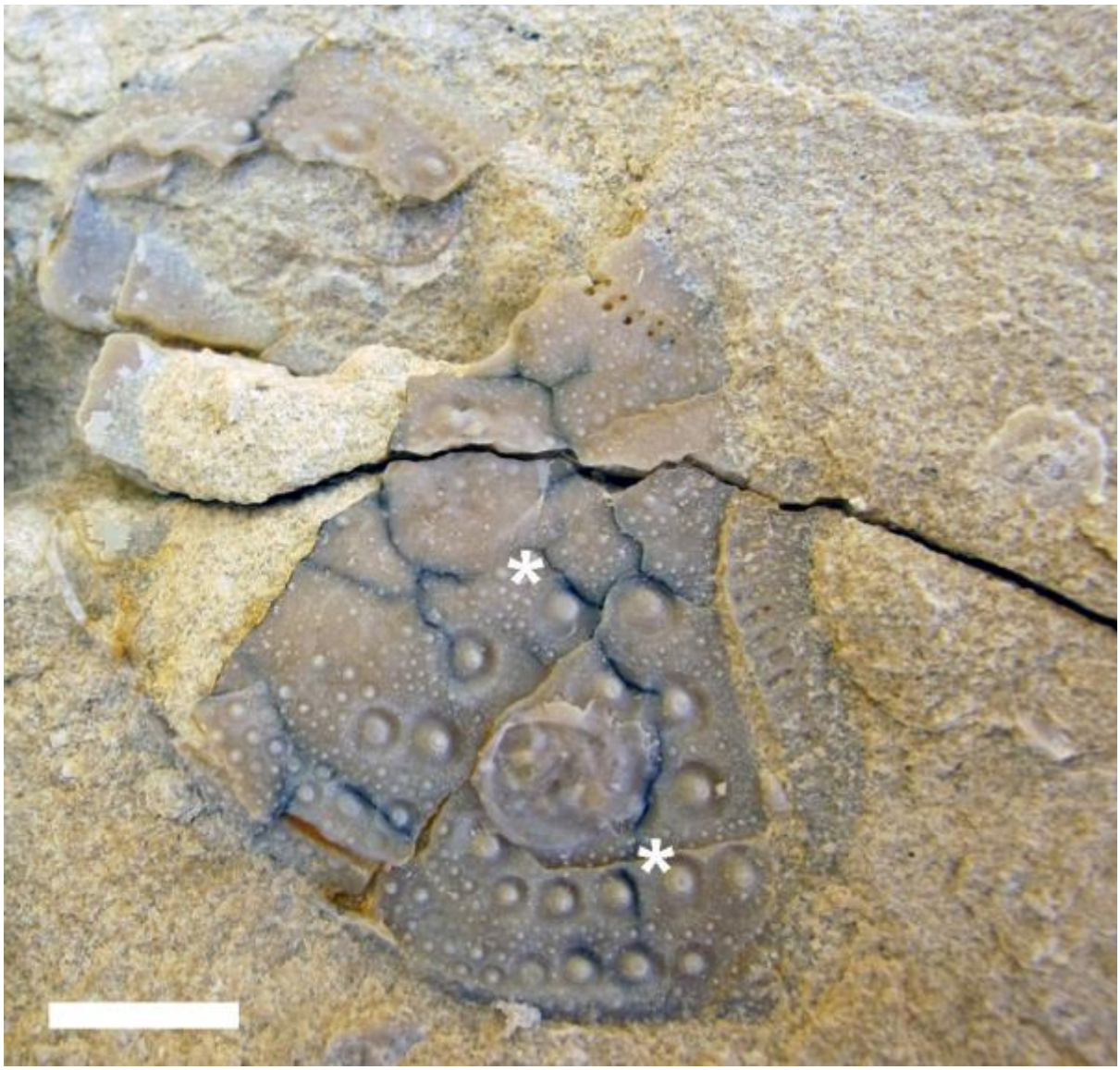

Fig. 3. Field photograph (Locality 1) of UF 277885, the apical surface of the spatangoid echinoid *Eupatagus* sp. encrusted by the thecidoid brachiopod, thecidoid sp. indet. (see also Fig. 4C, F).

Attached brachiopod valves are indicated thus (*). Scale bar represents 10 mm.

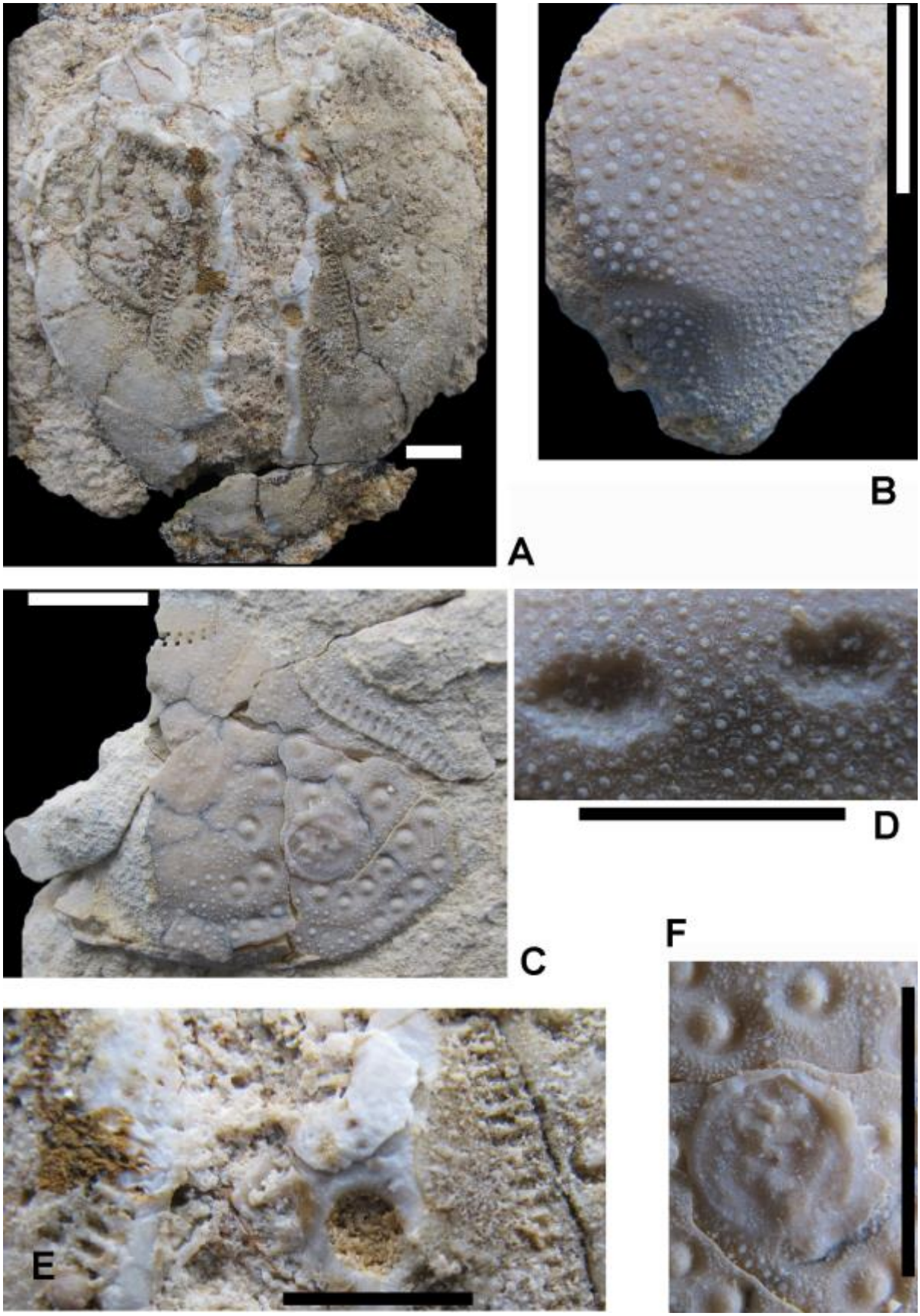

Fig. 4. Variously infested echinoids from the Upper Oligocene Antigua Formation of Antigua. All

from Locality 1 unless stated otherwise. (A, E) UF 277887 (Locality 2), *Eupatagus* sp., apical surface with boring and worm tube. The inner column of pore pairs in the right posterior ambulacral petal is pierced by a small round hole, *Oichnus* isp. The remnants of a serpulid worm tube are apparent more adapically adjacent to the left posterior petal (A). (B, D) Depressions in test fragments. (B) UF 279143, shield-shaped depression with unsculptured bottom, upper centre of image. (D) UF 277 886, lozenge-shaped depressions bearing echinoid primary and secondary tubercles. (C, F) UF 277 885, apical surface of *Eupatagus* sp. encrusted by the thecidoid brachiopods, thecidoid sp. indet. (compare with Fig. 3). (C) Specimen as collected; rotated about 45° clockwise from Figure 3. Prominent brachiopod slightly towards lower right from centre; second specimen left of centre (note plate sutures apparently truncated by edge of valve). (F) Detail of the brachiopod attached valve, umbo towards top of page. Specimens uncoated. All scale bars represent 10 mm.